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POLLINATORS OF AN ENDEMIC AND ENDANGERED SPECIES, *MAMMILLARIA GAUMERI* (CACTACEAE), IN ITS NATURAL HABITAT (COASTAL DUNE) AND IN A BOTANICAL GARDEN

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Abstract

Mammillaria gaumeri (Britton & Ross) Orcutt (Cactaceae), an endemic plant of the Yucatan Peninsula, is included by the Mexican government in the list of species that require special protection. Its natural habitat is now restricted to fragmented areas and protection programs involve botanical gardens in growing individuals rescued from disturbed areas. Little information is available on the reproductive characteristics of this species and nothing is known of its pollinators. We investigated the visitors of *M. gaumeri* flowers, collecting and observing bee species in its natural habitat (i.e., coastal dune) and in a botanical garden, where coastal dune vegetation had been created. Observations were made on plants whose density was artificially increased by grouping flowering individuals. At each site, we: 1) collected insects visiting the flowers; 2) recorded number of visits; and 3) video-recorded bee movements on the flowers. As expected, the number of bee species and visitation frequency were higher at the botanical garden than at the coastal dune. After landing on a flower, bees either inspected the anthers or dived among them. These behaviors, carried out by all observed species, seemed related to the state of the anthers (full or empty of pollen) and stigma lobes (opened or closed). Specifically, visits lasted longer when anthers were full of pollen and stigma lobes were opened. The same bee species recorded on the dune were also recorded at the botanical garden, suggesting that the artificial dune at the botanical garden offered suitable conditions for the natural pollinators of this endangered cactus.

Resumen

Mammillaria gaumeri (Britton & Rose) Orcutt (Cactaceae) es endémica de la Península de Yucatán y está incluida en la lista de especies que requieren protección especial por decreto del gobierno de México. Presenta un hábitat restringido en áreas fragmentadas y los programas de protección consideran el rescate de individuos de áreas perturbadas para crecerlos en jardines botánicos. De la poca información disponible sobre las características reproductivas de esta especie, no se conoce nada de sus polinizadores. En este estudio, nosotros investigamos los visitadores de las flores de *M. gaumeri* y observamos y colectamos las especies de abejas en su hábitat natural (duna costera) y en un jardín botánico, donde el hábitat de la duna costera ha sido imitado. Las observaciones fueron hechas en plantas cuya densidad fue aumentada artificialmente con varios individuos en floración. En cada sitio: 1) colectamos los insectos que visitaron las flores; 2) registramos el número de visitas; y 3) filmamos los movimientos de las abejas sobre las flores. Como esperábamos, el número de especies de abejas y la frecuencia de visitas fueron mayores en el jardín botánico que en la duna costera. Al aterrizar sobre una flor, las abejas se comportaron de dos diferentes maneras: ya sea que ellas inspeccionaban las anteras o se zambullían entre ellas. Estos comportamientos, realizados por todas las especies visitadoras, parecen estar relacionados con el estado de las anteras (llenas o vacías de polen) y a la posición de los lóbulos del estigma (abiertos o cerrados). Específicamente, las visitas duraron más tiempo cuando las anteras estaban llenas de polen y los lóbulos de los estigmas estaban abiertos. Las mismas especies de abejas se colectaron en ambos sitios, lo que sugiere que la duna artificial del jardín botánico también ofrece condiciones adecuadas para los polinizadores naturales de este cactus amenazado.

Key Words: botanical gardens, Cactaceae, endangered cactus, endemic cactus, *Mammillaria gaumeri*, pollinators.

When dealing with the conservation of endangered plant species, research usually has focused on habitat preservation (Hall and Gillespie 2004), reserve design (Deltoro et al. 2004), demography for short-term population management (Fox and Gurevitch 2000), and the possibility of reproduction in botanical gardens for future reintroduction in their natural range of distribution (Perini and Tornadore 2004). But, it is also frequently

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reported that endangered plant species experience reproductive failure that may be strongly related to the loss of pollinators (Aronne and Wilcock 2004). Many species may vegetatively reproduce, especially when pollinators are rare or absent and flower fertilization is low. However, pollination (i.e., cross-pollination) of flowering plants provides the enormous benefit of gene flow in the population and helps to maintain the species' ability to respond to a changing environment (Proctor et al. 1996; Price 2002).

To formulate effective strategies for management and conservation, it is essential to understand the ecological and evolutionary nature of plant-pollinator interactions. Notwithstanding that pollinators of many plant species are not yet identified (Kearns et. al. 1998), there is already evidence that a deficit of pollinators in fragmented habitats threatens plant populations and plant diversity (Lennartsson 2002).

Regarding plant conservation and reintroduction, one potential problem is that some native pollinators may have disappeared. Nonetheless, most flowering plants are pollinated by moderate to high numbers of insect species, and most floral visitors usually visit many different hosts (Corbet 1997; Kearns et al. 1998). Thanks to the multiple pollinators observed for the majority of plant species, "new" pollinators might adopt a plant if its original pollinators are absent. The adoption of endangered species by alternative pollinators may also be crucial when trying to propagate them under artificial conditions, as in botanical gardens. Thus, priorities for research programs should include the identification of native pollinators as well as other possible pollinators of the threatened plant species.

Mammillaria gaumeri (Britton & Rose) Orcutt (Cactaceae, tribe Cacteae) is a globular cactus endemic to the northern coast of Yucatan. This species is under special protection in the Protection of Natural Resources Document by the Mexican government (NOM-059-ECOL-2001). It grows only in some restricted areas, due to fragmentation of its natural habitat by human disturbances such as urbanization, cattle-range management, and agriculture (Durán et al. 1998). Some studies deal with its distribution and abundance, seed germination, and seedling survival (Leirana-Alcocer and Parra-Tabla 1999; López-Jiménez 2001; Cervera et al. 2006), but accurate information on its reproductive biology is still lacking. Our aim was to identify the native pollinators of this rare species, through the collection of pollinators in one of its natural habitats, the coastal dune scrubland. We were also interested in the flower visitation rate in a botanical garden, where plants rescued from disturbed areas have been preserved on an artificial dune. Between these two sites we compared pollinator species and visitation frequency. We described the bees' behavior to infer each species' interest in the resources offered by the flower and possible elements crucial in flower selection by pollinators.

Methods

We conducted field observations on a natural population of *Mammillaria gaumeri* in the coastal dune scrubland of San Benito (21°19′10″N, 89°30′40″W) and in an artificial coastal dune recreated at the Centro de Investigación Científica de Yucatán (CICY) Botanical Gardens in the city of Mérida (21°02′38″N, 89°38′22″W). The subject of the study is a small globular cactus that grows on exposed areas as well as under cover of vegetation.

At the two sites, the micro-habitats were very similar, but differed in the respective surroundings. On the coastal dune, the vegetation was mainly characterized by small bushes and succulents that can reach heights from 3 to 5 m, and common species were *Coccoloba uvifera* (L.) L. (Polygonaceae), *Cordia sebestena* L. (Boraginaceae), *Bravaisia berlandieriana* (Nees) T.F. Daniel (Acanthaceae), *Agave angustifolia* Haw. (Agavaceae), *Opuntia dillenii* (Ker Gawl.) Haw. (Cactaceae) *Acanthocereus tetragonus* (L.) Hummelinck (Cactaceae) and *Myrmecophila tibicinis* var.*christinae* Carnevali & Gómez-Juárez (Orchidaceae); the area surrounding the dunes included urban areas and natural vegetation. The CICY Botanical Garden recreates many habitats on an area of 27,000 m^2, and maintains 107 families and 592 plant species. Around it, land was urbanized.

We established a 2-m × 2-m observation area at each site. At San Benito, where we located about 4 flowering individuals of *M. gaumeri* on the dunes in open areas, 7 plants growing in pots were added. Plant density at this study site was 0.86 individuals per m^2, so density was increased to 2.75 m^{-2}. At CICY Botanical Gardens, 9 plants were growing in pots and located in open areas (plant density = 2.25 m^{-2}). Flower density was then increased compared to natural conditions, but kept constant at both sites (about 15 opened flowers during observations).

We collected specimens and made observations during the early dry season (January 27 to February 3, 2005), which lasts from November to February and is marked by an alternation of full sun and cloudy days, with infrequent precipitation and strong winds. Because Hymenoptera are often inactive on cloudy days, we used data from sunny days only. Status of flowers (open/closed) was recorded every hour for nine flowers on four plants.

Considering weather conditions (around midday clouds appeared) and flower opening, we based comparisons on visitation frequency between 10:30 and 12:00. The number of flower-

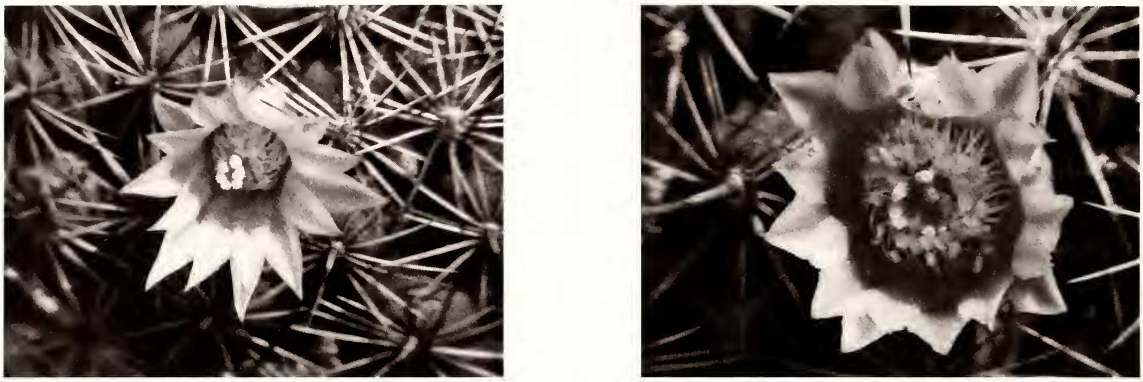

FIG. 1. Flowers of *Mammillaria gaumeri*. The anthers are curved towards the stigma; the lobes are still close in the flower on the left and open in the flower on the right.

visiting bees was recorded during one day at each site; attention was directed to bees landing independently on each flower by only one observer at each site. Temperature and relative humidity were also recorded during observations, using a digital thermo-hygrometer (Deltha Ohm, HD201-1; Italy).

The video-recording of some visits (n = 31) with a digital video-camera (Sony, DCR-TRV80E; Japan) equipped with magnifying lens provided data on: landing surface elected by the bee; flower characteristics at the moment of the visit (empty/full anthers, open/closed stigma lobes); bee behaviors on the flower; and visit duration. Video-recording was done on January 27, 29 and February 3, 2006 only when bees were approaching flowers. Total duration of the video record was about 30 min, obtained during 9 hr of observations.

Due to difficulties of identification related to their small size, bees were divided into three recognizable classes: small black bees, megachilid bees, green bees. Additionally, some scattered observations at both sites and specimen collection were done, on sunny days, from January 15 to February 10, 2005.

Statistical analysis was performed using Statistica (StatSoft Inc., Tulsa, Oklahoma, USA) and following Zar (1974).

RESULTS

Characteristics of *Mammillaria gaumeri* Flowers

The flowers of this species are of a pale color, with whitish-yellow petals and light yellow anthers. Anthers are very numerous and curved towards the stigma (Fig. 1). The stigma has four lobes that changed in color from yellow to reddish-pink and from a closed to an open stance. Flowers were fully open (Fig. 2) during the central hours of the day (12:30–15:30). However, we observed bees entering flowers with petals only slightly opened.

Number of Bee Species

Table 1 reports all species collected at the two sites. We collected two species at San Benito: an Apidae, *Ceratina* Latreille sp. 1, and a Colletidae, *Hylaeus quadratifera* (Cockrell). Also, we observed an ant, which apparently inspected a flower, and we saw a winged wasp (possibly a Sphecidae or a Mutillidae) visiting a flower.

We collected five bee species at CICY Botanical Gardens. Among them, there was one of the bee species collected at San Benito (Colletidae, *Hylaeus quadratifera*), another Apidae belonging to the genus *Ceratina* Latreille sp. 2, and other three species belonging to two families (Megachilidae, *Megachile* Latreille sp.; Halictidae, *Dia-*

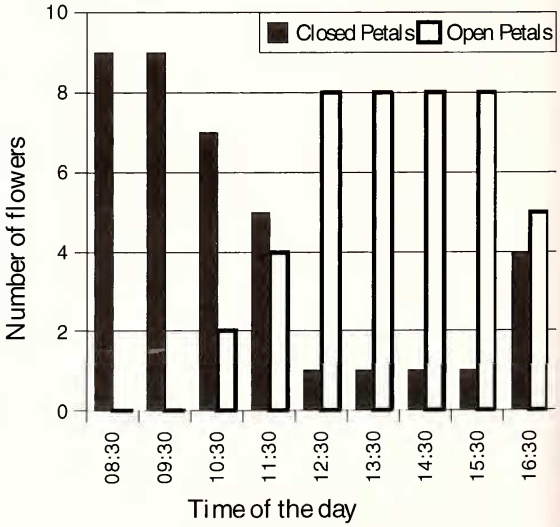

FIG. 2. Opening time of the nine flowers under observation on a sunny day.

TABLE 1. BEE SPECIES COLLECTED DURING OBSERVATIONS ON FLOWERS OF *MAMMILLARIA GAUMERI*. Classification following Michener (2000).

Family	Subfamily	Genus	Species	SAN BENITO	CICY Botanical Gardens
Apidae	Xylocopinae	*Ceratina* Latreille, 1802	Unknown 1	Present	—
			Unknown 2	—	Present
Colletidae	Hylaeinae	*Hyleaus* Fabricius, 1793	*quadratifera* (Cockrell)	Present	Present
Halictidae	Halictinae	*Dialictus* Robertson, 1902	Unknown	—	Present
		Augoclora Smith, 1853	Unknown	—	Present
Megachilidae	Megachilinae	*Megachile* Latreille, 1802	Unknown	—	Present

lictus Robertson sp. and *Augochlora* Smith sp.). During observations, no ant or wasp visited the flowers, although some were present at the site.

Observed species correspond to the bee classes as follows: Small black bees = *Ceratina* sp. 1, *Ceratina* sp. 2, *Hylaeus quadratifera; Dialictus* sp.; Megachilid bees = *Megachile* sp.; Green bees = *Augochlora* sp.

Visitation Frequency

At both sites, climatic conditions during observations were optimal for bee activity, with full sun and high temperatures. At San Benito, temperatures were lower (range 27.0–29.1°C) than at CICY Botanical Gardens (32.0–34.7°C); relative humidity was higher at San Benito (64.3–67.9%) than at CICY Botanical Gardens (36.9–45.1%)., the number of visits recorded at CICY Botanical Garden was 2 times higher than that recorded at San Benito ($X^2 = 5.32$, $P < 0.05$). While in San Benito small black bees were responsible for all the visits (n = 16), at CICY Botanical Garden they made 27 out of 32 visits (84%). The other visits were distributed among megachilid bees (3 visits) and green bees (2 visits). (These observations were very limited, however [from 10:30 to 12:00, one day per site].)

Description of Visits

The following descriptions regard the behavior of *Ceratina* sp. 1, *Ceratina* sp. 2, *Hylaeus quadratifera*, and *Megachile* sp.

Bees landed on the flower rapidly: in 69.3% of the cases (n = 26), they landed mainly on the petals and walked to the anthers; in 19.2% of the cases, they landed on the stigma lobes, then move to the anthers, whereas in 11.5% of cases, they landed directly on the mass of anthers. Petals were the more frequent landing surface ($X^2 = 15.46$, $P < 0.001$). After reaching the anthers, pollinators a) inspected them with their antennae (42% of cases; n = 31), or b) dove immediately among them (42%), and in a few cases, we recorded c) both behaviors (16%). No statistical differences among the frequency of the three behaviors emerged ($X^2 = 4.13$, n. s.).

Mean and SE of visit duration of each case is reported in Table 2. The first strategy (i.e., inspecting the anthers) consisted of very short visits: bees landed on the flower as described above and quite immediately flew away. The second strategy (i.e., diving among anthers) included the bee disappearing under the anthers, a lapse of time during which movements were perceived from oscillation of anthers and stigma,

TABLE 2. DESCRIPTIVE STATISTICS OF VISIT DURATION. Observations based on: bee behavior, flower characteristics (anthers and stigma lobes), and bee group. Data obtained from analysis of video-recorded images. Statistical analysis between groups is reported in the text.

	Average (seconds)	SE (seconds)	N
Bee behavior			
inspecting	2.18	0.50	11
diving	11.08	1.39	13
Anthers characteristics			
full of pollen	3.08	0.80	13
empty of pollen	9.87	1.43	16
Stigma lobes characteristics			
opened	9.35	1.44	17
closed	3.25	0.84	12
Bee group			
megachilid bees	8.60	3.44	5
small black bees	6.46	1.10	24

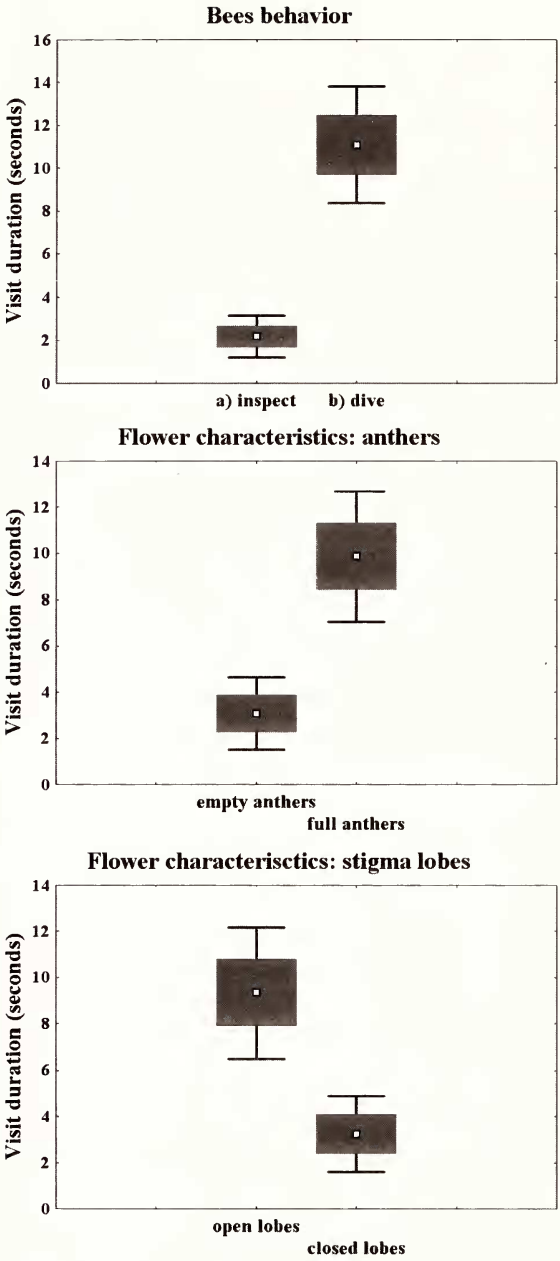

FIG. 3. Average duration of visits depending on bee behavior and floral characteristics (anthers and stigma lobes). Data were obtained from analysis of video-recorded images. Upper graph: visit duration depending on behavior; middle graph: visit duration depending on anthers (full or empty); lower graph: visit duration depending on stigma lobes (opened or closed). Data are means (open squares) ± SE (gray squares) ± 1.96 × SE.

and partial visualization of the bee among the stamens. After that, they emerged and cleaned/moved pollen grains to the legs, possibly resting for a few seconds, while lying on the anthers or on the petals, and then they flew away. The difference in visit duration between the two behaviors was statistically significant (Mann-Whitney z adjusted = −4.186, n 1 = 11, n 2 = 13, $P < 0.001$; Fig. 3, upper graph). There also was a significant difference between visits to flowers with full or empty anthers (Mann-Whitney z adjusted = −3.454, n 1 = 13, n 2 = 16, $P < 0.001$; Fig. 3, middle graph) and with opened or closed stigma lobes (Mann-Whitney z adjusted = 2.996, n 1 = 17, n 2 = 12, $P < 0.005$; Fig. 3, lower graph). When lobes were opened, flowers received 58.6% of visits (n = 29); when stigma lobes were closed, flowers received the 41.4% of visits. In 16 out of 25 visits, the body of a small black bee touched the stigma lobes, while it happened in 4 out of 5 visits for megachilid bees.

DISCUSSION

This preliminary study identified some of the pollinators of an endangered and endemic cactus of the Yucatan Peninsula, both in its natural habitat and in a botanical garden, where its habitat conditions were recreated. *Mammillaria gaumeri* can flower many times during a year, a trait shared with other, more common species of *Mammillaria* (Bowers 2002). Flowering several times within a year may increase the probability of pollination by enabling flowers to encounter pollinators under different environmental conditions.

Ceratina species, as well as *Hylaeus quadratifera* and *Dialictus* sp., accounted for most visits to *Mammillaria gaumeri* flowers at both sites. The tribe Ceratinini (Apidae, Xylocopinae) consists of small and slender species, similar to the world-wide subfamily Hylaeinae (Colletidae), a group of minute to moderate-sized, mostly slender bees with a limited yellow or white mark on the face (Michener 2000). *Ceratina* usually nest in dead plant material, such as hollow or pithy stems or burrows made in rotten woody vines or stems. As do many Allodapinae in the Old World Tropics and *Hylaeus*, they tolerate exposure and highly variable nesting temperatures (Roubik 1989). Michener (1970) found more nests of *Ceratina* in the introduced plant species of gardens than in normal vegetation, which may account for the ability of this genus to invade non-natural areas and consequently provide the pollination service needed.

The two species (*Ceratina* sp. and *Hylaeus quadratifera*) collected on the dune scrubland were the only flower visitors during observations. On the dune, the vegetation provides plenty of nesting substrate (dead plant material). We can imagine that in such an environment a strong relationship between a pollinator and this plant species may exist (flowers are small, pale, located at surface level, often hidden by other plants). Both bee species are characterised by a small size

(four to six millimetres long) and by the fact that pollen is carried in the crop moistened with nectar. This feature may justify the observed behaviour on the flowers: bees diving among anthers may be searching for the nectaries. Nectar is even the main resource found in Hylaeinae nests, so accurate measurement of nectar crop in *M. gaumeri* population may indicate its importance as a nectar resource for the corresponding population of bees. The percentage of individuals observed touching the stigma (64%; n = 31), as well as the ones landing on it, accounts for a potentially good pollination service.

The simulated coastal dune habitat at CICY Botanical Gardens (about 30 km from San Benito) has favored the establishment of the bees found on the dune. At CICY Botanical Gardens many different habitat have been created, such as tropical dry deciduous forest, dry deciduous forest with columnar cacti, and coastal dune scrubland; the high amount of flowering species may also attract more bee species. This is actually confirmed by the bee collection on *M. gaumeri* made at this location and by the significant higher visitation rate recorded compared to the natural coastal dune in San Benito. Again more information on *M. gaumeri* resources may explain such a high rate of visit, considering the diverse flowering plants present at the site and the possible competition among them.

Megachilidae are famous for collecting pollen on the underside of the abdomen. They do not line their cell, but use building materials as lead or petal pieces, chewed leaf pulp, hairs, nectar, resin, pebbles, mud and combinations of these (Michener 2000). Provisions are not shaped in any form, but pollen is loose; some species are pollen specialist (Roubik 1989). They are bigger than *Ceratina* and *Hylaeus* and this may result a disadvantage for the flower because bee movement among the anthers may damage the tissues. Also, considering that in their cells the only provision is pollen, it would be interesting to verify whether these bees were feeding on the nectar or collecting pollen when diving among the anthers. Halictinae includes some of the commonest bees; they mainly nest in the soil, in banks or flat soil, or rarely in rotting wood (but *Augochlora* females do). Provisions are usually firm, sub-spherical and lie on the ventral surface of the cell. The majority of species are polylectic (Michener 2000). Few individuals belonging to these two families have been recorded, but they are probably more widespread than supposed. It would be especially interesting to compare the collection habits of these bees with those species observed on the dune, to estimate their potentiality as pollinators of *M. gaumeri*. In fact, the intensity or quality of pollination may be affected if pollinator species changed (Corbet 1997).

Although there were some differences in foraging and nesting characteristics, all species performed different behaviors depending on the state of the anthers, as well as that of the stigma lobes. These differences highlight the importance of recognition by individual bees of the flower status and possibly also of the reward to be found in the flower. Flower attributes need to be further studied in order to infer the information obtained by the approaching bees and for a better understanding of bee reactions when landing on a flower. This was only a preliminary work, but its results have raised many questions related to the recovery of the natural populations of *M. gaumeri* and its pollinators, and its cultivation in botanical gardens.

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